FTD-HC-23-0244-72

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## ON INFORMATION PROCESSING IN THE VISUAL SYSTEM OF VERTEBRATES. I

by

W. Seelen

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by Joint Publications Research Services

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English pages: 47

Source: Kybernetik, (Cybernetics), Vol. 7, No. 2, 1970, pp. 43-60.

Requester: ASD

UNCLASSIFIED

Security Classification

**DOCUMENT CONTROL DATA - R & D**

*(Security classification of title, body of abstract and indexing annotation must be entered when the overall report is classified)*

1. ORIGINATING ACTIVITY (Corporate author)
Foreign Technology Division
Air Force Systems Command
U. S. Air Force

2a. REPORT SECURITY CLASSIFICATION
UNCLASSIFIED

2b. GROUP

3. REPORT TITLE
ON INFORMATION PROCESSING IN THE VISUAL SYSTEM OF VERTEBRATES. I

4. DESCRIPTIVE NOTES (Type of report and inclusive dates)
Translation

5. AUTHOR(S) (First name, middle initial, last name)
W. Seelen

6. REPORT DATE
June 1970

7a. TOTAL NO. OF PAGES
47

7b. NO. OF REFS

8a. CONTRACT OR GRANT NO.

b. PROJECT NO. 6090-02

c.

d.

9a. ORIGINATOR'S REPORT NUMBER(S)
FTD-HC-23-0244-72

9b. OTHER REPORT NO(S) (Any other numbers that may be assigned this report)

10. DISTRIBUTION STATEMENT
Approved for public release; distribution unlimited.

11. SUPPLEMENTARY NOTES

12. SPONSORING MILITARY ACTIVITY
Foreign Technology Division
Wright-Patterson AFB, Ohio

13. ABSTRACT

In the domain of form recognition the human visual system surpasses by far the capacity of actually existing technical devices designed to serve the same purpose. Therefore it appears advantageous to undertake a communication-theoretic function-description and structure-description of the biological system in order to gain suggestions for the solution of technical problems and in order to make possible the adaptation of technical apparatus to human beings. Over and above this an understanding of visual information processing will probably permit inferences to be drawn regarding the functioning of fairly large parts of the brain since the information picked up by the peripheral sense organs is processed in similarly structured networks in the cerebrum [1]. The following investigation is based essentially on the electrophysiological studies of Hubel and Wiesel on the visual cortex of cats and monkeys [1-5]. In consequence of the similar structure of the human visual system, conclusions regarding the processing of visual information in humans is possible, within certain limits. The experimental results available up to now have been very fragmentary in consequence of the extraordinarily difficult conditions of experimentation.

DD FORM 1 NOV 1473

UNCLASSIFIED

ii

| 14. KEY WORDS | LINK A | | LINK B | | LINK C | |
|---|---|---|---|---|---|---|
| | ROLE | WT | ROLE | WT | ROLE | WT |
| Information Processing<br>Vertebrate<br>Vision<br>Binocular Vision | | | | | | |

ON INFORMATION PROCESSING IN THE VISUAL SYSTEM OF VERTEBRATES. I

[Paper by Dr. Werner von Seelen, Institute for Vibration Research of the Fraunhofer Society, Karlsruhe, West Germany, Kybernetik, German, Vol. 7, No. 2, June 1970.]

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## 1. Introduction.

In the domain of form recognition the human visual system surpasses by far the capacity of actually existing technical devices designed to serve the same purpose. Therefore it appears advantageous to undertake a communication-theoretic function-description and structure-description of the biological system in order to gain suggestions for the solution of technical problems and in order to make possible the adaptation of technical apparatus to human beings. Over and above this an understanding of visual information processing will probably permit inferences to be drawn regarding the functioning of fairly large parts of the brain since the information picked up by the peripheral sense organs is processed in similarly structured networks in the cerebrum [1].

The following investigation is based essentially on the electrophysiological studies of Hubel and Wiesel on the visual cortex of cats and monkeys [1 - 5]. In consequence of the similar structure of the human visual system, conclusions regarding the processing of visual information

in humans is possible, within certain limits.

The experimental results available up to now have been very fragmentary in consequence of the extraordinarily difficult conditions of experimentation. In the following an attempt will be made to embed these previous findings, with regard to form-vision, in a communication-theoretic model and an attempt will also be made to indicate possibilities for the quantitative description of some phenomena. In the present state of knowledge a description having complete experimental support appears scarcely possible so that in some areas research must be considered speculative and to be of the nature of a working hypothesis.

## 2. The Physiologic Structure of the Visual System.

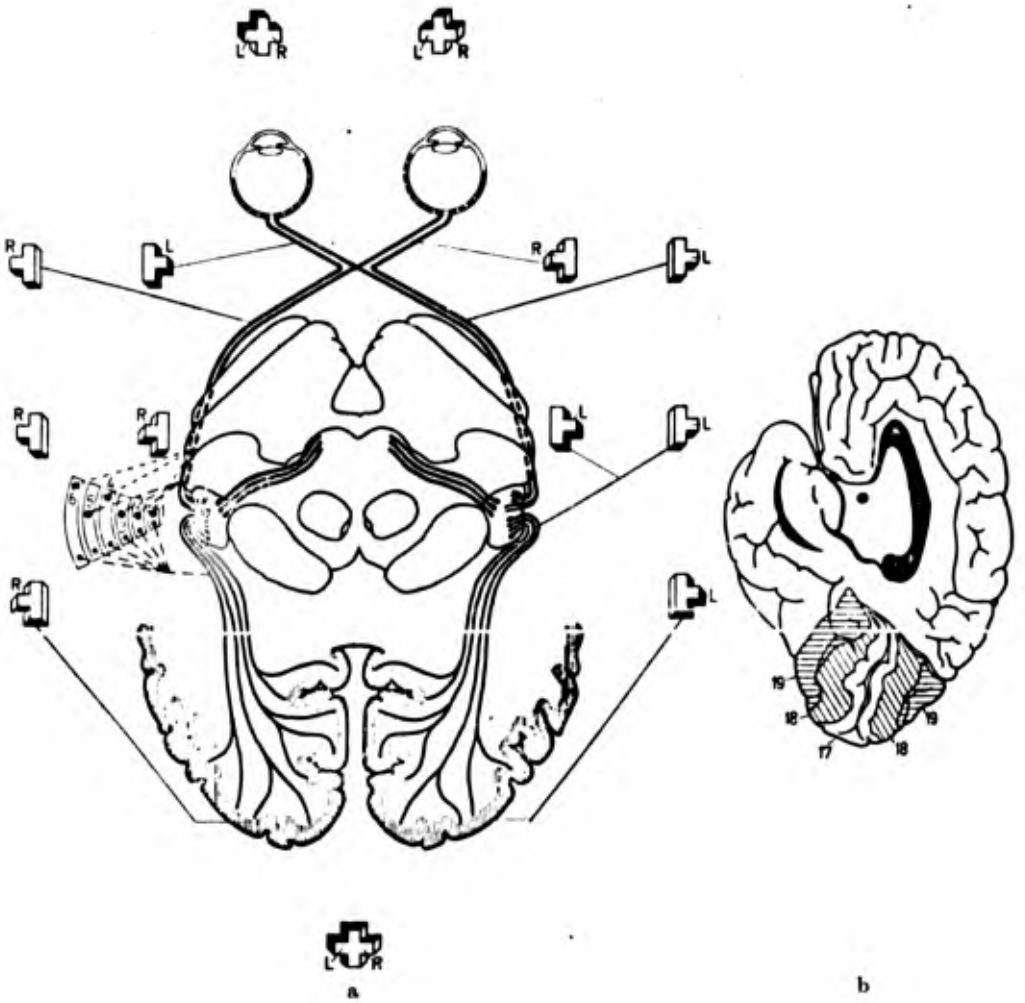
The processing of visual information in vertebrates takes place in several systems connected one after the other; the three first of these systems have up to now been at least partially investigated experimentally: the retina with the associated neural network, the geniculate body and the visual cortex. Figure 1a shows the structural schema of the visual system; the parts of the system which have been referred to are denoted by A, B and C.

By means of the optical apparatus an inverted image of the environment is produced on the retina and is scanned in man by around $10^7$ receptors whose diameters amount to 2-8$\mu$ . In terms of their external shape the receptors are subdivided into rods and cones; the former permit twilight vision under low light intensity, the $6 \times 10^6$ cones are used for daylight and color vision. The distribution density of the two varieties of receptor is distinctly dependent upon location. In the area centralis ($\sim 1^\circ$ in man) the cones predominate, in the marginal region the rods. The total distribution density diminishes as one approaches the periphery.

The receptors absorb light quanta and transform the input stimulus into electric potentials; the spectral absorption range lies between 400 and 700 m$\mu$. The visual angles of the two eyes, each amounting to about 160°, overlap in those vertebrates which were involved in the experiments which shall be discussed in the following pages.

The receptors are connected to a multi-layered neural network consisting of diverse cell types; the cells of this neural network interact upon one another in inhibition and excitation, depending upon their mutual distance. The outputs of this network, in which [the network] a preprocessing of the position-dependent input stimulus distribution takes place, are the axons of ganglionic cells which form the optic nerve, itself consisting of around $10^6$ fibers. The retina is functionally halved by a vertical meridian. The nerve fibers of the outside half go to the brain hemisphere on the same side while the fibers from the inner half of the retina cross behind the eyes and pass to the opposite half of the brain. The transformations of the visual system at various positions are shown in Figure 1a using a cross

as an example. The first switching station of the visual tract is the corpus geniculatum (B). In Figure 1a there is shown a cross-section (denoted by $B_s$) of this six layered area. The superimposed neural layers are alternately connected with the interior (or exterior) retina-half of each eye [6]. The corpus geniculatum is on the one hand connected with the parts of the brain which control the eye movement, on the other hand it is connected with the area striata (C) of the cerebral cortex; this region is characterized by a layered structure which is clearly parallel to the cerebral surface in a manner which partially associates certain cell types to the individual layers. Functionally the area striata may be divided into three regions: the areas 17, 18 and 19. Their limits in the human brain are indicated in Figure 1b by means of variable shading. It is probably with the neural nets of this region that the decisive transformations of form-vision are realized. This cortical region has connections to higher association levels of the brain in which somewhere the recognition of the pattern is localized. However up to the present observations have been confined only to the first three processing levels of the visual system.




Figures 1a and b: Diagram of visual information processing (a) and location of the cortex areale (b) in the human central nervous system.

## 3. On the Methodology of the Measurements and of Quantitative Description.

### 3.1. Problem Statement and Description Possibilities.

The visual system which serves vertebrates for orientation in a three-dimensional environment is to be interpreted as a pattern recognizing system. In the following pages arbitrary distributions of luminosity serve as the pattern; problems of spatial and color vision are not investigated. All patterns occurring in the environment have to be arranged in pattern classes. The patterns of a pattern class are thus not in general identical but are characterized by a series of characteristic signs by means of which they are placed in a particular class [7]. Consequently in the process of classification it is not possible to carry out a simple test of identity between known and unknown patterns, but similarities must be evaluated. Thus for example a tree is recognized as such even when the momentarily presented form of it has never been previously seen by the beholder. In detail, two stages of processing must be distinguished in pattern recognition:

1. The determination of the characterizing signs which most satisfactorily describe the patterns.

2. The assignment, on the basis of its sign value, of the pattern to a certain class.

Most of the hitherto extant experiments with the visual system relate to the preprocessing mentioned under point 1. Therefore the research described in the following pages is related primarily to this problem-category and specifically with the following questions:

1. What function principle is employed in the three first stages of the visual system?

2. What properties does the system possess with respect to the formation of sign-classes and invariance-classes?

3. How is the system structurally realized?

The quantitative description of a neural network aims at establishing with the greatest possible exactitude the functional dependence of the output quantity upon input signal and upon the system parameters. Since the elements of the system, the neural cells, operate non-linearly it would be necessary to select a method of description which is also non-linear. However up to the present there has been no complete theory available which would permit a general description. In addition the number of available quantitative measurements is very small so that it has not been possible to check the exactness of a method of description by appealing to experiments. For such a procedure it is necessary that measurements should be made, inter alia, not only of the output frequency but also intracellularly

of the temporal history of the excitatory and inhibitory membrane potentials and the threshold values for the cells of a neural network. However, the experimental effort required for this is very great. Hence in what follows an attempt will be made to fit the previous findings into linear formulations, especially as it has been shown that in the domain of low light intensities and when variations of intensity remain small in proportion to the base-level, the linear methods of description are sufficiently exact [8, 9]. Beside the advantage of simple manipulation of the equations permitted by the linear approach, it also permits simple inferences to be drawn regarding the network structure (see Section 3.3.1). Further experiments must show whether a piece-wise linearization of the characteristic curve or the definition of a description function [10] are preferable to a general non-linear formulation.

In the case of a pulse-frequency modulated input signal, the deviation of the neuron characteristic from linearity has three causes.

1. The presence of a response threshold,
2. The finite integration time of the synapses, which has its effect especially in the case of low impulse frequencies at the input,
3. The refractory time [Refraktaerzeit] of the cells which manifests itself in the upper frequency range.

If one uses the characteristic between the threshold S and the range in which the refractory time needs to be taken into consideration, then despite the small integration time it is possible to carry out a linearization. The prerequisite for this is the assumption that the networks are strongly intermeshed, as occurs for example in the case of the eye, for which the integration with respect to time may be replaced by the formation of a family-mean taken over a large number of synapses, so that the effective input signal of a cell is only a slightly varying mean value [11]. Under these conditions, in a neuron network the i-th nerve cell having m input quantities may be described by means of

$$z_i(t) = \begin{cases} \sum_{j=1}^{m} b_{ij}\, y_j(t) - S & \text{für } \sum_{j=1}^{m} b_{ij}\, y_j(t) > S \\ 0 & \text{für } \sum_{j=1}^{m} b_{ij}\, y_j(t) \leq S \end{cases} \tag{1}$$

where $y_j(t)$ denotes the input signal, $b_{ij}$ denotes the coupling factor which characterizes the effect of the j-th neuron upon the i-th neuron and $z_i(t)$ denotes the output quantity of the i-th neuron. If one investigates the relations exclusively in the linearizable part of the characteristic at intensities which are large in comparison with the threshold, then Equation (1) becomes

(2) $$z_i(t) = \sum_{j=1}^{m} b_{ij} \cdot y_j(t).$$

For the entire system we have, in vectorial notation

(2a) $$\mathfrak{z} = \mathfrak{B}\,\mathfrak{y}.$$

The quantities y and z denote the input vector and output vector respectively; $\mathfrak{B}$ denotes the matrix of the coupling coefficients. In general the coupling factors are frequency-dependent and in consequence the output quantity of a neuron is derived by means of a convolution operation in the time domain. From Equation (2) one gets

(3) $$z_i(t) = \sum_{j=1}^{m} \int_{0}^{t} g_{ij}(\tau)\, y_j(t-\tau)\, d\tau.$$

The quantity $g_{ij}(t)$ is the impulse reaction function of the i-th neuron referred to the j-th input.

If $p = \psi + i\omega$ is a complex variable, then using Laplace transformation one gets from Equation (3)

(4) $$Z_i(p) = \sum_{j=1}^{m} G_{ij}(p)\, Y_j(p).$$

The quantity $G_{ij}(p)$ is called a transfer function. In a network having arbitrary mesh and m input and n output signals one has for the description of the entire system

(5) $$\begin{pmatrix} Z_1(p) \\ \vdots \\ Z_n(p) \end{pmatrix} = \begin{pmatrix} G_{11}(p) \dots G_{1m}(p) \\ \vdots \qquad\quad \vdots \\ G_{n1}(p) \dots G_{nm}(p) \end{pmatrix} \begin{pmatrix} Y_1(p) \\ \vdots \\ Y_m(p) \end{pmatrix}.$$

The goal of the experimental analysis of a network, as for example of the visual system, is thus the determination of the matrix of transfer functions characterizing the system. This quantity may be established by the measurement of the n impulse reaction functions for each of the m inputs and requires n X m measurements, assuming that no further simplifying assumptions

can be made.

3.2. On Measurement Methodology in the Visual System.

Experimental investigations of the visual system include both behavioral experiments and electro-physiological measurements. In the first mentioned aspect of the procedure the quantization of the stimulus response in animals presents a particularly difficult problem.

For this reason it is frequently the practice to determine only one point on the characteristic associated with the system being investigated: namely the sensitivity threshold under various conditions involving simple yes-no decisions. These investigations have often been carried out for the visual system of man [9]. More exact -- although experimentally more difficult -- are electro-physiological measurements of static and dynamic type.

During electro-physiological measurements the measurement probe is introduced (for example) into the axon of a ganglion cell and the response recorded as a function dependent upon the position of a small point of light upon the retina. The domain in which the point of light calls forth a reaction from the cell being investigated is called the receptive field. In the first processing stages of the system the receptive fields are approximately radially symmetric; they possess a stimulating central domain and an inhibitory peripheral field or conversely. The investigations relate both to steady states and to time-dependent transition processes. With dynamic measurements one usually uses the time-dependent jump function in both contrast directions with a variable geometric form for the stimulus. Thus for example the responses are recorded which are produced by ganglion cells in response to the turning on and off of geometric position-dependent patterns. In very many cases the system responds exclusively to dynamic stimuli. If the illumination of a receptive field-component produces a system response which dies away after some interval of time then it is called an on-reaction. If the response is a response to darkening then it is called an off-reaction. The nature of the dynamic response can be either independent of the inhibitory and excitatory domains within the receptive field or it can be subdivided according to excitatory and inhibitory areas. Apart from the switching-on processes, input patterns in motion are very effective stimuli for the visual system. The receptive fields constitute, in the present state of experimental technique, the most substantial method of description of the neural network within the visual system.

3.3. On the Theory of Neural Nets.

Equation (1) describes the input-output relation at a neural cell. Since the number of synapses can attain 4,000 the number of possible connections becomes very large and the description very complicated. However, numerous findings show that -- at least in the peripheral part of the nervous system -- this manifold of possibilities is not fully exploited but certain

interconnection schemata are maintained, in particular scattering, forward-inhibition and backward-inhibition. In Figure 2 the types of interconnection are represented by means of an example containing two elements.

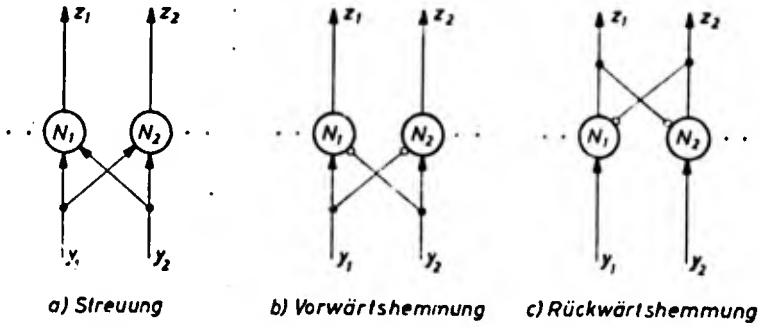



Figure 2. Coupling principles for neurons.
Key:
a) Scatter.
b) Forward-inhibition.
c) Backwards-inhibition.

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Arrows denote excitatory, small circles inhibitory inputs; a neural network contains in general all types of coupling. These coupling principles appear to be very important for the understanding of the total visual system; their quantitative description will therefore be briefly explained in the following section.

3.3.1. Static Case.

Assumptions:

1. The networks are linear.
2. The input and output quantities are independent of time.
3. The networks are homogeneous; i.e., all neurons are interconnected in the same way.
4. Neurons are either arranged in a line or in a surface and are interconnected with one another in a manner which is dependent upon their mutual distance; the position-dependent values of the coupling factors are described by the coupling function. In addition let us assume that m = n.

The first condition is exact only in certain regions, however it makes possible a synoptic description and facilitates understanding of the total system. The third assumption represents a usable approximation in the domain of the area centralis which is essential for form-vision. It facilitates description and experiment for in consequence of the homogeneity the diagonal values in Equation (5) are equal to one another so that only at the most n measurements are required for a description of the system.

If one assumes a neuron network with -- as in the eye -- the elements arranged in a surface, then for forwards-inhibition we get for the i-th element from Equation (2)

(6) $$z_i = y_i - \sum_{\substack{j=1 \\ i \neq j}}^{m} b_{ij} y_j, \qquad j = 1, 2, \ldots, m$$

or in vectorial notation

(7) $$\mathfrak{z} = \mathfrak{B}_v \mathfrak{y}.$$

For scattering networks we get

(8) $$\mathfrak{z} = \mathfrak{B}_s \mathfrak{y}$$

and in the case of backwards-inhibition the describing system of equations is

(9) $$\mathfrak{z} = \mathfrak{B}_R^{-1} \mathfrak{y}.$$

The matrices $\mathfrak{B}_v$, $\mathfrak{B}_s$ and $\mathfrak{B}_R$ contain as elements the coupling factors for the three types of interconnection. In connection with the backwards-inhibition coupling principle instabilities can occur; they occur whenever the condition Det $|\mathfrak{B}_R| = 0$ for the invertability of the coupling matrix in Equation (9) fails to be fulfilled [12]. Since the above systems of equations permit an estimation of the effects of system parameters only at the cost of great outlay of effort, a further assumption is introduced which, under the contemplated conditions, gives rise only to slight error [13]:

<u>The distribution density of the neuron field is assumed to be infinitely great.</u> Under this condition the fields are described in terms of the position coordinates r and s; $H_b(r,s)$ denotes the two-dimensional inhibitory density distribution in the case of forwards-inhibition and describes the effect of the input quantity at the position (r,s) upon the neighboring domains. $H_S(r,s)$ and $H_R(r,s)$ denote the corresponding quantities in the case of scattering and backwards-inhibition. From Equation (6) we get for the case of forwards-inhibition

(10) $$z(r,s) = \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} H_v'(r-w, s-x)\, y(w,x)\, dw\, dx$$

where

(11)
$$H'_v(r-w, s-x) = -H_v(r-w, s-x) + \delta(r-w, s-x).$$

If one selects as input quantity for a one-dimensional system a position-dependent periodic function

(12)
$$y(r) = k \cdot \cos r u_0,$$

then one gets as output quantity in the case of forward-inhibition

(13)
$$z(r) = k \cdot [1 - F(H_v(r))_{u=u_0}] \cos u_0 r,$$

where $F(H_v(r))$ represents the Fourier transform of the coupling function $H_v(r)$. The output quantity has the same position-frequency $u_0$ as the input quantity and is weighted with a frequency dependent factor. Thus the network achieves the same transformations for the position-dependent periodic functions as are achieved by the linear filter for time processes. The output quantities of these linear systems are calculable for the case of forward-inhibition by making use of the impulse reaction function in accordance with

(14)
$$z(r, s) = \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} g_v(r-w, s-x)\, y(w, x)\, dw\, dx.$$

The impulse reaction function $g_v(r,s)$ thus turns out on the basis of Equations (10) and (14) to be

(15)
$$g_v(r, s) = H'_v(r, s).$$

Hence the measurement problem for Equation (5) is reduced to the determination of the discrete coupling function. From Equations (10) and (14) one gets, using Fourier transformation

(16)
$$F(g_v(r, s)) = 1 - F(H_v(r, s)).$$

The quantity $F(g_v(r,s))$ is the 5 of the system which is frequently more suited for study of the network then are the corresponding functions in the upper range.

For the scattering we have

(16a) $$F(g_s(r,s)) = F(H_s(r,s)),$$

and for the case of backwards-inhibition one gets

(17) $$F(g_R(r,s)) = \frac{1}{1 - F(H_R(r,s))}.$$

In contrast to filters for time-dependent signals, the position filters corresponding to Equations (16), (16a) and (17), for a prescribed frequency response curve, can be realized in a very simple way.

It may be shown that backwards-inhibiting systems may be replaced by networks which are interconnected in accordance with the principles of scattering and forwards inhibition [12]. Hence in what follows only the two latter coupling principles are discussed in further detail. If in the case of forwards inhibition, which lies at the basis of Equation (11), direct positive coupling is replaced by a position-dependent scattering interconnection, then we have

(18) $$H(r,s) = H_s(r,s) - H_v(r,s)$$

and the impulse reaction function of the system is analogous to Equation (15)

(18a) $$g(r,s) = H(r,s).$$

The coupling function H(r,s) is thus the decisive quantity which determines the properties of the system. The position-dependent behavior may be interpreted in the visual system in accordance with Figure 3 as the difference between two bell-shaped curves of different breadth and height; an exponential drop-off of the coupling functions produces nearly quantitative differences. If the coupling functions are radially symmetric, the frequency response curves display the same property in the position domain and a one-dimensional description suffices. The reasons for these assumptions are explained in Section 4.1.2.

If in a forwards inhibitory system connected in accordance with Figure 2b the directly excitatory coupling is replaced by a position-dependent scattering having the profile

(19) $$H_s(r) = m_1 e^{-\frac{r^2}{R_1^2}}$$

and if the inhibition is described by

(19a) $$H_s(r) = m_2 e^{-\frac{r^2}{B_2^2}},$$

with

(19b) $$B_2 = k B_1,$$

then for the frequency response curve of the entire system we have

(20) $$F(g(r)) = \sqrt{\pi}\left[m_1 B_1 e^{-\frac{u^2 B_1^2}{4}} - m_2 k B_1 e^{-\frac{u^2 B_1^2 k^2}{4}}\right],$$

where u denotes the position frequency.

With regard to the character of the system, the following important cases are distinguishable:

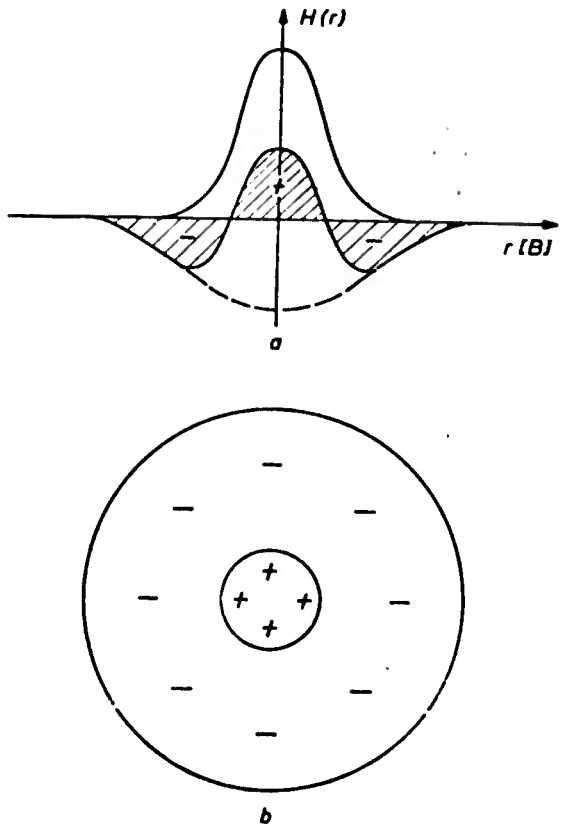
1. $m_2 = 0$, $m_1 \neq 0$, $B_1 \neq 0$. The network represents a low pass filter whose limiting frequency is high to the degree that $B_1$ is small.

2. $B_1 \to 0$, $H_s(r) = m_1 \delta(r)$, $m_2$ 0, $B_2$ 0. The system is a high pass filter whose lower limiting frequency is high according as $B_2$ is small.

3. $k > 1$, $m_1 > m_2$. The receptive field is positive at the center and negative along the boundary (Figure 3b), such a network has the character of a band pass. The band width is narrow to the degree that the difference $B_2 - B_1$ is small. The maximal value of the frequency response curve is derivable from Equation (20) at the frequency

(21) $$u_m^2 = \frac{4 \ln \frac{m_2 B_2^2}{m_1 B_1^2}}{B_2^2 - B_1^2}.$$

With $m_1 B_1 = m_2 B_2$ the mean value of the brightness (base brightness) is suppressed so that for differences of contrast in the images the full dynamic range of the system is available; this case is very essential in the nervous sytem. In Figure 4 curve (a) shows a band pass for $m_1 B_1 = m_2 B_2 = 1$ and curve (b) shows a band pass for $m_1 B_1 = 2$, $m_2 B_2 = 1$.




Figures 3a and b. Coupling function (a) and receptive field (b).

4. $k < 1$, $m_2 > m_1$. The receptive field has a negative center and a positive boundary region; the system displays band pass character, frequency response curve and output quantities are inverted in contrast with case 3 (Figure 4c).

The relationships described in points 3 and 4 are especially important for the analysis of the visual system. For the band passes shown

in Figure 4, their transformations in the upper range are displayed in Figure 5, using the example of the jump function. In the two-dimensional case a pattern may be reduced to its contour line. The amplitudes along the contour line depend upon the line's curvatures; with an appropriate design of the system, corners or sharp angles can be especially emphasized. Such a scattering-inhibition network can accomplish a useable preprocessing for pattern recognition whenever the patterns to be recognized in different classes are distinguishable by their position-frequency content [12].

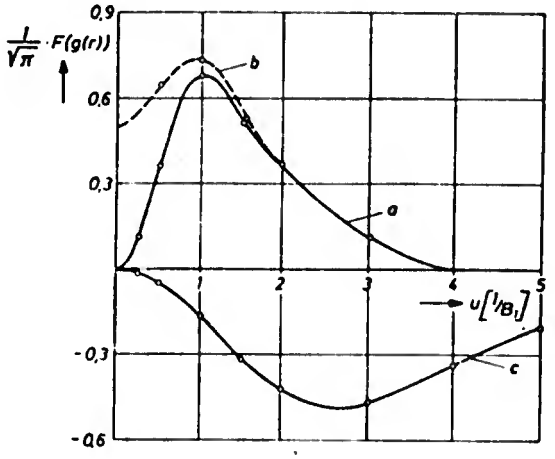



Figure 4. Local frequency response curve in non-normed form with $m_1 B_1 = m_2 B_2 = 1$ and $k = 3$ (a) as well as $k = 1/2$ (c). In curve (b) $m_1 B_1 = 2^1$ $m_2 B_2 = 1$ and $k = 3$.

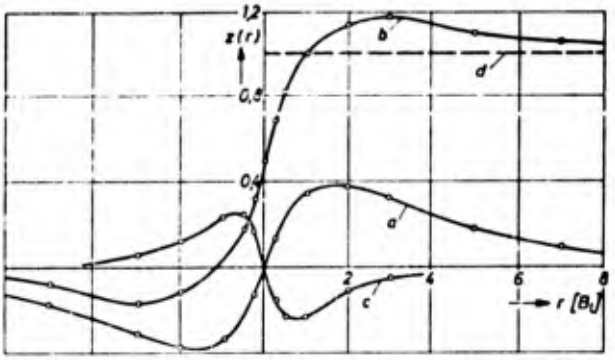



Figure 5. Jump responses of the band pass systems given in Figure 4. The associated curves are indicated by the same letters; curve (d) shows the input quantity.

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In this filtering, with a subsequent measurement of output power, only the absolute value of the Fourier transform is evaluated; if a local shift of the pattern occurs the output quantity is invariant with respect to this change of position. Rotation of the pattern is equivalent to a rotation of the Fourier transform through the same angle. If the coupling function of the system is symmetric, the output quantity of the filter is invariant with respect to rotations of the input distribution. If there is a dilatation of the pattern, with a signal being transformed from f(r,s) to f(cr,cs), then for the frequency response curve of the transformed pattern we have $F_r = \frac{1}{c^2} F\left(\frac{u}{c}, \frac{v}{c}\right)$, where F(u,v) is the Fourier transform of the signal f(r,s). If the classification of the pattern is accomplished by determining the power output within a specified band width then such a process is independent of the degree of dilatation. In the case of unsymmetrical coupling functions there occurs additionally a 12 and the rotational invariance is lost; however for this reason patterns are distinguishable depending upon their angular position. Thus the amplitudes of the output quantity can, depending upon the design of the system, be functions of the curvature of the contour line, of the angular position of the pattern and of its size [12].

3.3.2. Dynamic Case.

Assumptions:

1. The input quantities are time-dependent.

2. The coupling factors are dependent upon the frequency $\omega = 2\pi/T$. The frequency response curve of the coupling factors is described for scattering by $A_s(p)$, for inhibition by $A_v(p)$. The values of $A_s(p)$ or $A_v(p)$ are independent of the distance.

3. The frequency response curves of the coupling factors are approximated by means of low pass filters of the first order, whose time constants are distinguishable in inhibition ($T_2$) and scattering ($T_1$).

Condition 2 probably represents a simplification in the visual system; however hitherto there has been no precise analysis of the dependence upon distance of $A_s(p)$ or $A_v(p)$. Besides the effect of homogeneity, condition 3 is decisive in determining the function principle of the entire system, for this assumption determines the character of the dynamic responses and the latter are very important for the understanding of the transformations taking place in the visual system. The experimental findings supporting assumption 3 are discussed in Section 4. In consequence of the radial symmetry of the fields in the first levels a one-dimensional description suffices.

a) Switching-on a stimulus. Let the position-dependent behavior of the coupling of a network be described in the temporally steady state by

$$H(r) = m_1 e^{-|r|/B_1} - m_2 e^{-|r|/B_2}. \tag{22}$$

Relative to the coupling determined by Equations (19) and (19a), the mathematical description is simplified in the network described by Equation (22); qualitatively both systems are equivalent. What coupling functions are realized in various animals has hitherto not been exactly established. The quantities $m_1$ and $m_2$ give, as in Equations (19) and (19a), the maximal values of the coupling functions for dispersion and inhibition, $B_1$ and $B_2$ denote the values at which the coupling functions of the two types of interconnection are reduced to the (1/e)th parts of the maximal values. For the test stimulus the jump function was selected, in the interest of clarity:

$$y(r, t) = \sigma(r) \cdot \sigma(t). \tag{23}$$

In analogy to Equation (10) one gets at the output, in the case of a time-dependent input quantity:

(24) $$z(r,t)=\int_0^t\int_{-\infty}^{\infty} H(r-w,t-\tau)\,y(w,\tau)\,dw\,d\tau.$$

Using Equations (22) and (23) in Equation (24) one gets by applying the Fourier transformation

(25) $$z(r,t)=\frac{1}{4\pi^2}\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}\left(\frac{2m_1B_1e^{iur+i\omega t}}{(1+B_1^2u^2)(1+T_1i\omega)u\omega}-\frac{2m_2B_2e^{iur+i\omega t}}{(1+B_2^2u^2)(1+T_2i\omega)u\omega}\right)du\,d\omega,$$

if, on the basis of assumption 3, the frequency response curve of the coupling factors is describable by a low pass filter. Using the residue theorem one gets:

(26) $$z(r,t)_{r>0}=m_1B_1(1-e^{-t/T_1})\left(2-e^{-\frac{1}{B_1}r}\right)-m_2B_2(1-e^{-t/nT_1})\left(2-e^{-\frac{1}{kB_1}r}\right),$$

(27) $$z(r,t)_{r<0}=m_1B_1(1-e^{-t/T_1})e^{-\frac{1}{B_1}r}-m_2B_2(1-e^{-t/nT_1})e^{-\frac{1}{kB_1}r},$$

(28) $$T_2=nT_1$$

For the structure of the system four cases are distinguishable, using the same integral over the dispersion coupling functions and inhibition coupling functions ($m_1 B_1 = m_2 B_2$); of these four cases the two following are especially important in the visual system:

1. $n>1$, $k>1$. The center of the receptive fields is positive, in the boundary region inhibition preponderates. The jump response has "on"-character. In Figure 6 the jump responses for $r>0$ are plotted for various time points with $k = n = 3$ and with distance measured in coupling breadths $B_1$. The responses are symmetrical

with respect to the intersections of the curves with the ordinate.

2. $n < 1$, $k < 1$. A stimulus in the center of the field has an inhibiting effect, at the boundary the effect is excitatory and the jump response has "off"-character. In Figure 7 the position-dependent responses of the system at various time points, after applying the input stimulus $\sigma(r)$, are plotted for $r < 0$. The distance is measured in the coupling breadths $B_1$ of the dispersion. The symmetry points of the curve are to the right of the ordinate.

The jump responses are, as in the experimental findings, clearly above the output quantity in the steady state. By means of a threshold the static response can be suppressed and the dynamic reaction can be detected. The positional and temporal location of the maximal value of the output quantity depends upon the values k and n.

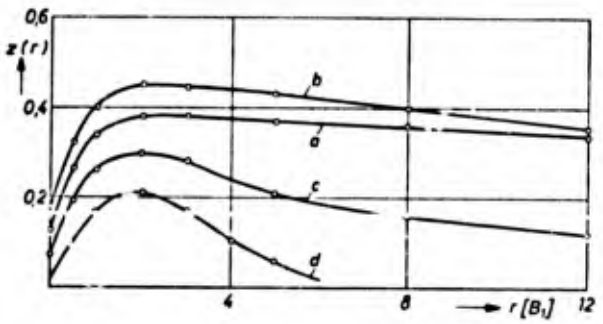



Figure 6. Position-dependent responses of an inhibition-dispersion system, for $r > 0$, to a position-dependent and time-dependent jump function having amplitude "1" at different time points after activation. The curves a - d are the system responses at the time points $t = 1/2\ T_1$, $t = T_1$, $t = 2\ T_1$ and $t = 6\ T_1$.

b) Motion of a stimulus. Moving patterns are very effective input stimuli; in the optical cortex, pattern motion is at times even a necessary condition for system response. The following explanation and quantitative description is based, as in Section a) on the differing time constants of inhibition and dispersion.

Let the input quantity y(r) move with constant velocity $\bar{v}$ over the field and let it be described by

$$y(r, t) = \delta(r + \bar{v}t), \tag{29}$$

then from Equation (24) we get for the Fourier transform of the system response:

$$F_R[F_t(z(r,t))] = F_R[F_t(g(r,t))] = 2\pi\delta(\omega - u\bar{v}) \cdot \left[\frac{2m_1 B_1}{(i + \bar{D}_1^2 u^2)(i + \bar{T}_1 i\omega)} - \frac{2m_2 B_2}{(i + \bar{D}_2^2 u^2)(i + \bar{T}_2 i\omega)}\right]. \tag{30}$$

The inverse transformation of Equation (30) in the upper range is to be interpreted as an impulse reaction function for systems whose input quantities move with constant velocity.

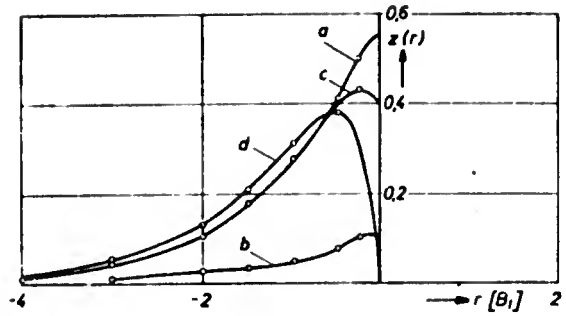



Figure 7. Position-dependent jump responses of an inhibition-dispersion system for $r<0$ at various time points after switching off the jump function $\sigma(r)$. In curve (a) $k = 1/3$, $n = 1/6$, $t = T_1/4$, in curve (b) $k = 1/3$, $n = 1/6$, $t = 2\,T_1$, in curve (c) the parameters are $k = 1/3$, $n = 1/4$, $t = T_1/4$, curve (d) shows the system response before switching off ($t = 0$).

---

The quantity $\bar{\nu}$ can also be a function of position. In the $F_R$ [$F_t(g(r,t))$], u,$\omega$-system the frequency response curve runs along a straight line; in the u,$\omega$-plane the rise of this straight line depends upon the velocity. In consequence of the motion and in spite of radially symmetric coupling in the local domain there occurs a phase-frequency curve [sic] and consequent dispersion.

If, for reasons of clarity and bearing in mind the findings which we want to interpret, we select the system response to a moving jump $\sigma(r - \bar{\nu}t)$, then using the residue theorem we get from Equation (24)

$$
\begin{aligned}
z(r,t)_{(r+\bar{v}t)>0} = {} & 2m_1 B_1 - \frac{m_1 B_1^2}{B_1 - T_1\bar{v}}\, e^{-\frac{1}{B_1}(r+\bar{v}t)} \\
& + \frac{2m_1 B_1 (T_1\bar{v})^2}{B_1^2 - (T_1\bar{v})^2}\, e^{-\frac{1}{T_1\bar{v}}(r+\bar{v}t)} \\
& - 2m_2 B_2 + \frac{m_2 B_2^2}{B_2 - T_2\bar{v}}\, e^{-\frac{1}{B_2}(r+\bar{v}t)} \\
& - \frac{2m_2 B_2 (T_2\bar{v})^2}{B_2^2 - (T_2\bar{v})^2}\, e^{-\frac{1}{T_2\bar{v}}(r+\bar{v}t)},
\end{aligned}
\tag{31}
$$

$$z(r,t)_{(r+\bar{v}t)>0} = \frac{m_1 B_1^2}{B_1 + T_1 \bar{v}} e^{-\frac{1}{B_1} r} - \frac{m_2 B_2^2}{B_2 + T_2 \bar{v}} e^{-\frac{1}{B_2} r} \tag{32}$$

With

$$T_1 \bar{v} = p B_1 \tag{33}$$

and with Equations (19b) and (28) one gets in place of Equation (31) ard Equation (32), with the same integral over both coupling functions, where the mean value of the luminosity is suppressed ($m_1 B_1 = m_2 B_2$)

$$\begin{aligned} z(r,t)_{(r+\bar{v}t)>0} = & -\frac{1}{2(1-p)} e^{-\frac{1}{B_1}(r+\bar{v}t)} \\ & + \frac{p^2}{1-p^2} e^{-\frac{1}{pB_1}(r+\bar{v}t)} \\ & + \frac{1}{2\left(1-\frac{pn}{k}\right)} e^{-\frac{1}{kB_1}(r+\bar{v}t)} \\ & - \frac{n^2 p^2}{k^2 - n^2 p^2} e^{-\frac{1}{npB_1}(r+\bar{v}t)}, \end{aligned} \tag{34}$$

$$\begin{aligned} z(r,t)_{(r+\bar{v}t)<0} = & \frac{1}{2(1+p)} e^{+\frac{1}{B_1}(r+\bar{v}t)} \\ & - \frac{1}{2\left(1+\frac{np}{k}\right)} e^{+\frac{1}{kB_1}(r+\bar{v}t)}. \end{aligned} \tag{35}$$

If the integrals over the coupling functions are different from one another then one gets according to Equation (31) still a further position-independent and time-independent equal component [Gleichanteil]. The character of the system can be changed by variation of the quantities k and n. In experimental investigations of the visual system the following two cases have, as in 3.3.2.a, shown themselves to be significant:

1. $n>1$, $k>1$. A stimulus in the center of the field has an excitatory effect, inhibitory at the boundary. Figure 8 shows various jump responses referred to a coordinate system moving with $\overline{\nu}$. The increase (proportional to velocity) in the jump response allows motion detection and a suppression of the static image by a simple threshold operation.

2. $n<1$, $k<1$. The central domain is inhibitory, the boundary excitatory. The curves d and e in Figure 8 show the system responses. The amplitudes drop with rising velocity. The individual curves are symmetric about the coordinate origin.

If one reverses the direction of the $\overline{\nu}$-vector then Equation (35) when multiplied by (- 1) and when given negative exponents describes the jump response to the right of the jump edge, i.e., in case 1 there is an amplitude reduction. In case 2 the amplitudes to the left of the jump edge are described by Equation (34) multiplied by (- 1) and having positive exponents; in this case 2 there occurs an increase in amplitude. Figure 9 displays the qualitative profile of the jump response of a neuron field referred to a coordinate system moving with $\overline{\nu}$, whenever the receptive fields of the cells have the form shown. In additive cooperation of the neurons of both field-types it is possible to achieve an amplitude elevation at the positions of the contrast jump, independently of the contrast direction or -- when the contrast is given in advance -- independently of the direction of motion (so long as the negative parts of the responses are reduced or eliminated). Thus, with the aid of a non-zero threshold a suppression of immobile images can take place in a subsequent level. The vanishing of the stabilized retinal image can thus be interpreted by means of the mechanism which has been described.

c) Motion reactions in the case of combination of fields. In mammals on- and off-reactions already occur in the retina in a receptive field and in general an on-response is to be associated with the positive portion and an off-reaction with the negative portion. Such a field may be interpreted as the overlapping of two similar fields, one of which generates an on-reaction and the other an off-response. Both types of field can for example have a stimulating center and an inhibiting peripheral field.

The on-off reactions in a field can also be produced by the interaction of neurons with two different field types (e.g., in accordance with Figure 9). In this field combination there must likewise be produced a

complete suppression of stationary images while patterns variable in time and patterns in motion are detectable. The conditions required for this are equality of the constants k for both field types and larger values of n in fields corresponding to Figure 9a in contrast to those corresponding to Figure 9b. In contrast to stationary image suppression with fields of like type, in the present case the threshold at which the resting response is suppressed is independent of the contrast strength of the input pattern.

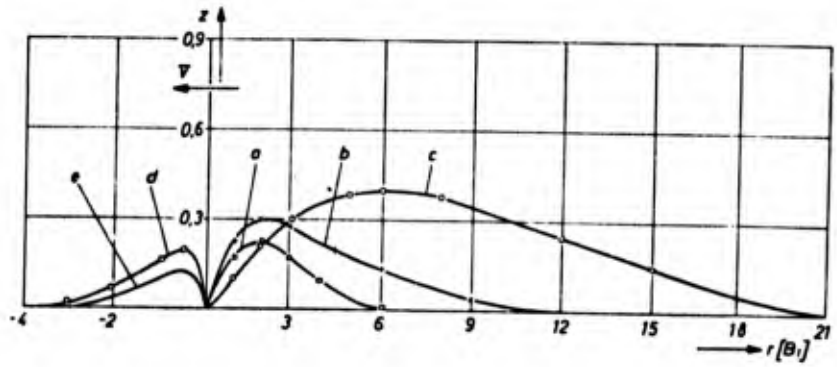
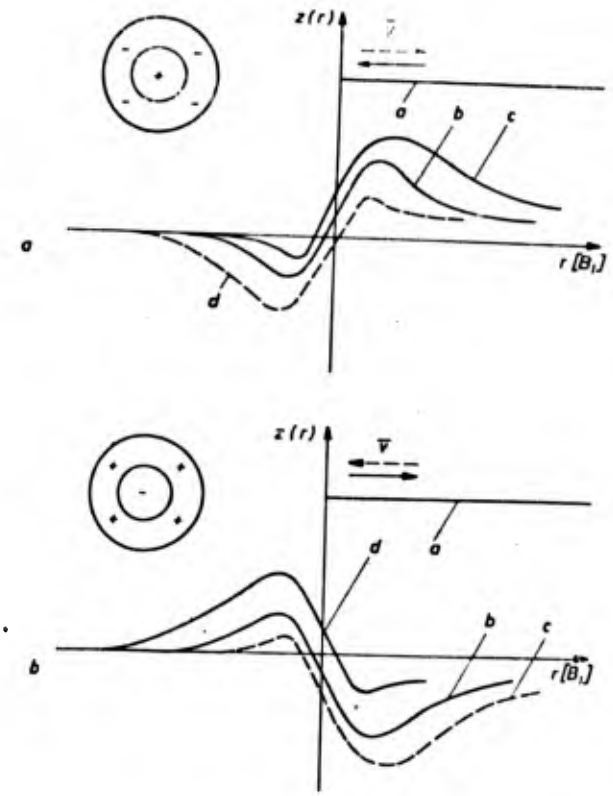



Figure 8. Jump responses dependent upon location at various velocities of the input quantity, referred to a coordinate system moving with $\overline{v}$. The curve parameters have the values k = n = 3, p = 0 (a); k = n = 3, p = 1/2 (b); k = n = 3, p = 3 (c); k = n = 1/3, p = 0 (d); k = n = 1/3, p = 1/2 (e).




Figures 9a and b. Position-dependent jump responses in the neuron field for $k > 1$, $n > 1$ (Figure 9a) and $k < 1$, $n < 1$ (Figure 9b) for uniformly moving stimulus. In both figures curve a denotes the input stimulus, curve b the response at $\bar{\nu} = 0$, curves c and d the responses for motion of the jump to the left or to the right.

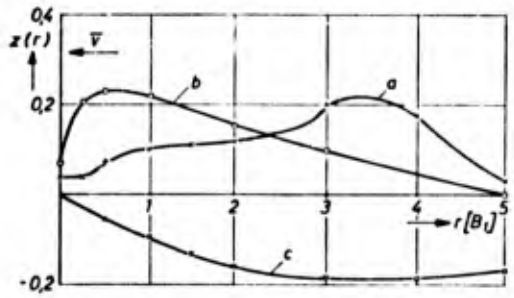



Figure 10. Responses of a neuron system for $r > 0$ to a position-dependent jump function, in motion with $\overline{\nu}$, at the input referred to a coordinate system (a, b) which is moving with it; the curve c shows the system response for $\overline{\nu} = 0$.

It is not possible to draw an unambiguous inference regarding the combination of various field types merely from the character of the response of a system to a mobile jump function at the input; for this it is necessary to refer to the entire profile of the dynamic reaction. If, for example, a system consists of neurons whose receptive fields have arisen by addition of both fields in accordance with Figure 9, then by a suitable choice of the parameter k it is possible to generate a receptive total field with negative center and positive margin, although the system responses to a mobile jump function at the input correspond to those of Figure 9a. Figure 10 shows the mobile responses of two such systems for the following parameters of the combined partial fields A and B: $n_A = 2$, $k_A = 3$ and $n_B = 2$, $k_B = 1/5$, $p = 2$ (curve a); the coupling functions diminish exponentially and are so constituted that the like-stimulus [Gleicherregung] is suppressed. The breadth $B_1$ of the coupling function which describes the stimulus in the field according to Figure 9a is equal to the breadth of the inhibiting coupling function in the field according to Figure 9b. In curve (b) of Figure 10 $k_A = 3$, $n_A = 5$, $k_B = 1/5$, $n_B = 2$ and $p = 0.5$; the curve (c) describes the jump response for $p = 0$. As shown by the position-dependent profile of the mobile responses in accordance with Figure 8, a decrease in contour sharpness is bound up with the motion. By means of the above described combination of different field types this unsharpness can be reduced by means of appropriate parameter selection (Figure 10b).

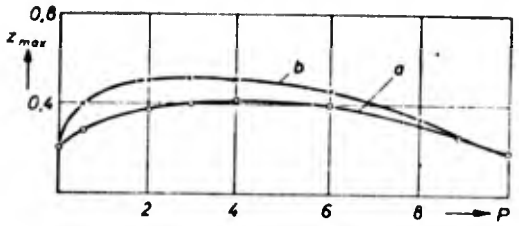



Figure 11. Maximal values of the jump responses in a neuron field at different velocities of the input stimulus for k = n = 3 (a) and k = 3, n = 5 (b).

In Figure 11 the maxima of the jump responses are plotted with respect to the velocity-proportional factor p; over extensive ranges, for the selected parameters, the extreme value is only slightly dependent upon the velocity.

In the visual system no velocities occur which are constant over fairly large ranges as was assumed in the preceding computation. However the formulations employed are suitable for deriving the transformations associated with real eye movements so long as the profile of the motion is known. The results computed in the preceding provide an estimate of the transformations under real boundary conditions.

3.3.3. Optimal Systems.

With the theory of statistically optimal systems it is possible to derive the theoretical limit of performance in systems for various reception problems relative to previously defined criteria of goodness. In addition this theory establishes the structures of the optimal systems. In consequence of the high level of performance capability in optical information processing it is to be expected that structural similarities should occur between visual and optimal systems. For this reason a special case of multiple detection will be treated below. An essential component of optimal systems is the statistically adapted filter, with which under certain assumptions the signal-to-noise ratio is to be maximized.

a) Statistically adapted (matched) filters. In the reception of a position-dependent signal perturbed in the local domain by white Gaussian noise the signal-to-noise ratio at a specific point in the (r,s)-plane is maximized by a filter which satisfies the condition

(36) $$F(y(r,s)) = F^*(y(r,s))$$

so long as the coupling function is symmetric [14]. $F^*(y(r,s))$ is the conjugate-complex Fourier transform of the unperturbed input signal y(r,s), which may therefore be assumed to be known. With Equation (18a) one gets

(37) $$F(H(r,s)) = F^*(y(r,s)).$$

The quantity H(r,s) describes the effect of a neuron at the position (0,0) upon the neighboring element. If one defines the effect of the position (r,s) on an element in the position (0,0) as the coupling function $\check{H}(r,s)$, then we get in place of Equation (36) with $\check{H}(r,s) = H(-r, -s)$ and

(38) $$F(\tilde{H}(r,s)) = F^*(H(r,s))$$

(38a) $$F(g(r,s)) = F^*(H(r,s)).$$

Thus one obtains for the matched filter

(39) $$\tilde{H}(r,s) = y(r,s).$$

The interconnection thus corresponds to the brightness distribution of the signal; here H(r,s) can be composed of stimulating and inhibiting regions, as long as the signal contains positive and negative deviations from a basic level of illumination. Depending upon the nature of the coupling function, we get for the Fourier transform of the output quantity generated by the unperturbed signal

(40) $$F(z(r,s)) = F^*(\tilde{H}(r,s)) \cdot F(y(r,s))$$

or

(41) $$F(z(r,s)) = F(H(r,s)) \cdot F(y(r,s)).$$

Equation (40) describes the cross-correlation of coupling function and signal while Equation (41) characterizes the filtering process. For the perturbed output quantity we have

(42) $$F(z(r,s)) = F^*(y(r,s)) \cdot F(y_e(r,s)),$$

where $y_e(r,s)$ is the signal y(r,s) after additive superposition of the perturbation. Hence the matched filter and in consequence, according to Equation (42), the special cross-correlator may be realized in a simple way. In this filtering process the signal shape is lost; at a specific point there arises, in the presence of an input signal, merely an intensity maximum. In

the case of an unsymmetrical coupling function the conjugate-complex Fourier transform of the signal in Equation (36) also involves a phase factor.

b) Multiple detection. Hypotheses: let there be given a two-dimensional signal source for which out of m possible signals only one appears at the output. Let the perturbation be white noise with Gaussian density distribution of the amplitudes.

A system is sought which decides which signal is present and which minimizes the mean risk of decision error on the basis of Bayes theorem. It is assumed that all erroneous decisions involve equal costs [14, 25].

One gets as a solution the maximum-likelihood-detector, whose structure is derived from the decision rule for signal recognition. The quantity represents the transposed vector of the n-dimensional perturbed input signal, the quantity $z_j$ is derived from the input signal according to

(43) $$z_j = \tilde{\eta}\,\mathfrak{B}_j,$$

where $\mathfrak{B}_j$ symbolizes the m weighting factors for the j-th signal whose position-dependent profile corresponds to the unperturbed j-th input signal.

The decision rules are: Determine the value of k for which

(44) $$z_k = \tilde{\eta}\,\mathfrak{B}_k = \max_{j=1}^{m} (\tilde{\eta}\,\mathfrak{B}_j), \quad j = 1, 2, \ldots, k, \ldots, m$$

and test whether

(44a) $$\tilde{\eta}\,\mathfrak{B}_k \geq c_k.$$

The character of the perturbation and the signal energy enters into the constant $c_k$. The expression $\tilde{\eta} \cdot \mathfrak{B}_k$ is interpretable as a filtering process for which the Fourier transform of the impulse reaction function is equal to the conjugate complex Fourier transform of the k-th input signal.

Thus we get for the optimal system a set of matched filters at whose outputs the maximal value is determined. If the maximum occurs at the k-th filter then the k-th input signal is decided upon, as long as the filter output quantity exceeds a threshold $c_k$ -- below the threshold a null signal is perceived. Figure 12 shows the structural schema of the system, the quantities $F_1$, $F_2$ ... denote the filters; $c_1$, $c_2$, ... are threshold-value elements.

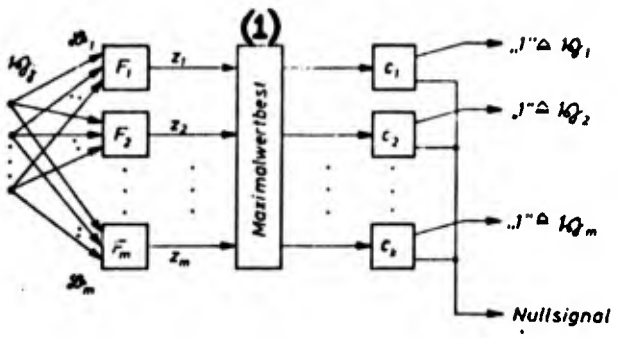



Figure 12. Optimal multiple detection system.
Key:
1. Maximal value determination.

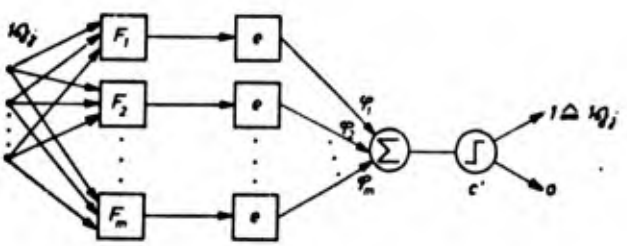


Figure 13. Optimal binary detection system.

If one modifies the condition so that it is only necessary to specify whether one of the m signals is present or not then the decision rule is:

Test whether

(45) $$\sum_{j=1}^{m} \varphi_j \cdot e^{\tilde{\nu}\vartheta_k} \gtrless c',$$

describes once again the filtering process, is the weighting factor into which there enters the character of the perturbation and the signal energy, c is a threshold. Figure 13 shows the structure of such a system; the parts designated e are amplifiers with and exponential characteristic ["with an exponential characteristic"? Error in original text]. They are realizable in the lower intensity range by means of neurons. If one interprets the m signals as a shape-element that can have either diverse positions, directions or sizes, then the system in Figure 13 represents, under the conditions mentioned at the outset, the optimal system which is invariant with respect to position, rotation or size.

In what follows the derived equations will be used to interpret the physiological findings and will be modified in accordance with the particular boundary conditions.

The findings evaluated below are selected under the aspect of shape-seeing and derive essentially from research on the visual system of the cat. Since the visual system of man is similarly structured, inferences by analogy are within limits admissible and psychophysical experiments may be drawn into the discussion. The interpretations are based upon three essential assumptions which are supported by the experiments described in Sections 4.1 - 4.3:

1. In the entire visual system there exist networks which are interconnected in accordance with the principles of inhibition and stimulation (dispersion).

2. The stimulation and inhibition types of coupling have distinguishable time constants.

3. The networks are homogeneous in the regions, important for shape-seeing, associated with the area centralis.

The principle of shunt inhibition [15] is not used in the explanation since there is not enough observational data to permit distinguishing the types of coupling employed here; moreover, some specific properties of shunt inhibition are also explicable by the temporal structure of the signals and the profile of the neuron characteristics in subtractive inhibition [15, 11].

## 4.1. The Retina.

### 4.1.1. Experimental Results.

The following summarized findings are marked with K whenever they derive from research on the retina of the cat. Measurements on the human visual system are indicated with M. The electrophysiological investigations relate exclusively to the layer of the ganglionic cells.

a) (K) In the retina the luminosity distribution on the receptor grid is transformed in the ganglionic cell layer into a position-dependent pulse-frequency distribution. This transformation -- which is not a 1:1 mapping -- involves the horizontal cells, bipolar cells and amacrine cells [16].

b) (K) To each ganglionic cell there is associated an approximately radially symmetric receptive field which is stimulating in the central region and inhibiting in the periphery or conversely. The fields overlap and increase in their size from some minutes of arc in the area centralis to up to 1 - 6° at the boundary of the retina [16].

c) (K) Within a receptive field-center excitability decreases toward the boundary. In this region, under high stimulation, the algebraic sum of the responses $z_1$ and $z_2$ of two individual stimuli is greater than the reaction $z_s$ in the case of simultaneous application of both stimuli; in this special case one gets $z_s = k_0 (z_1 + z_2) + z_0$ with $k_0 < 1$. In the outer field excitability (or the inhibitory reaction) generally attains a maximum and vanishes in the boundary zone [17, 18].

d) (K) Most ganglionic cells respond preferentially or exclusively to time-variable stimuli in the associated receptive field, some ganglionic cells with large receptive fields react preferentially to continuous stimulation. If a ganglionic cell responds to the switching on of a light stimulus with a higher pulse-sequence frequency then the reaction is called an on-response. The same reaction to switching off is called an off-response [17].

e) (K) At a ganglionic cell, under stimulation which was jump-shaped with respect to time, times of latency were measured in the positive central region of the receptive field in dependence upon light intensity varied in equal steps. The times of latency were $t_L$ = 93, 36, 22 and 15 msec at a background illumination of 2 mc [17].

f) (K) The size of a receptive field center increases, for small-area stimulation, with the intensity of stimulation; with

increasing background illumination [here called "Grundbeleuchtung" instead of "Hintergrundbeleuchtung" as everywhere else] the central region is narrowed [17].

g) (K) The field size and the regions of dynamic response are independent of the light intensity of the stimulus, its surface area and the total illumination of the retina [17].

h) (K) Stimuli in the positive (stimulating) region of a receptive field generate an on-response; in the negative (inhibiting) part of the field an off-reaction, in the transitional region one gets both types of response [17].

i) (K) If the illumination of the positive central region of a field, accompanied by simultaneous background illumination, produces an on-response then a reduction of the background illumination in conjunction with the same stimulus will produce an on-off-reaction; increasing the strength of the stimulus causes the same type of response as does an increase of the stimulated area in conjunction with constant background illumination. In negative central regions of receptive fields the reactions are equivalent. Thus the effect of the outer field is reduced by the background illumination and increased by increasing stimulus intensity and stimulus surface area [17].

j) (K) Under stimulation in both the outer field and in the central region of a receptive field (the stimulus being applied in each case to a small circular area) the stronger stimulus suppresses the response of the cell to the weaker input quantity. When both stimuli are of equal strength the pulse frequencies for both types of response are reduced and the times of latency are increased [17].

k) (K) If stimulus over a small surface area elicits a strong on-response with a weak off-component then the off-response can be eliminated by increasing the background illumination -- the on-component being at the same time only slightly changed [17].

l) (K) If an off-response is elicited in the central region of a receptive field then a second stimulus in the central region will interrupt the reaction of the ganglionic cell for the duration of the second stimulus [17].

m) (K) In positive and negative central regions the response thresholds and the times of latency are equal for on-responses and they are also equal for off-responses [17].

n) (K) The fusion frequency for flickering light, at which the temporal resolution of light flashes vanishes, is strongly dependent upon the intensity; for rods flashes are resolved up to a maximum of 20 per second, for cones up to 70 flashes per second are resolved; in man even 95 flashes per second are registered by the cones [16].

o) In the electroretinogram the b-wave (on-effect) has a smaller time of latency for cone-eyes than for rod-eyes. In the former eye-type the d-wave (off-effect) is more pronounced than in eyes in which rods preponderate [16].

p) (M) The eye carries out involuntary active motions which are corrective motions in following or fixating (saccades) as well as tremor motions which are independent of the former. Saccades have amplitudes up to 60' which are completed in around 0.1-0.3 sec; the time between two saccades lies in the range from 0.03-5 sec. The tremor has a frequency from 30 to 100 Hz with a mean maximal amplitude of 0.3' [16].

q) (M) The geometric resolution of two points of brightness increases with their light intensity [16].

r) (K) The mean discharge rate of the ganglionic cells for time-dependent sinusoidal light has a maximum at a stimulus frequency of f = 10 -- 15 Hz [18].

s) (K) For fields having a positive central region the limiting frequency of excitation for sinusoidal stimuli lies between 10 and 15 Hz, that of inhibition between 3 and 5 Hz; for a negative central region the limiting frequency for inhibition lies between 8 and 15 Hz [18].

t) (K) For stimulation of the retina with moving strip-patterns, for which there is, in the direction of motion, a position-dependent sinusoidal brightness distribution, the responses of the ganglionic cells are dependent upon the local frequency of the input pattern. For various local frequencies measurements were made of the contrast in brightness distribution; in this contrast there occurs, in association with a drift-velocity of the pattern amounting to one oscillation per second, a just audible modulation of the ganglionic cell frequency. The measurement curves are of the same type as curves a and b in Figure 4; they exhibit a band-pass behavior and are well approximable by the difference of two Gaussian functions [19].

u) (M) The subjective, still just perceptible contrast for stimulation with rectangular lattices is dependent upon the local frequency u and the time of presentation. In the local frequency

the ratio $V_0$ of the value of maximal sensitivity to the sensitivity for $u \to 0$ is around 5/2, if the time of presentation is 1,000 msec; at a stimulus time of 40 msec, $V_0 \approx 3/2$ [9].

v) (K) In the eye of the cat 80% of the ganglionic cells exhibit on-off-reactions, 15% on-responses and 5% off-reactions [16].

4.1.2. Discussion of the Results.

In the following, letters in parentheses denote the above described findings, from which our inferences are drawn.

1. The receptive fields of the retina represent sections through the coupling functions of the ganglionic cells at H(r,s) = 0. The position-dependent profile of these coupling functions has hitherto never been exactly measured but can only be inferred qualitatively from some publications; the approximate profile is shown (a, b, c) in Figure 3 [16, 18]. Equation (5) gives the measuring procedure for the exact determination of the coupling function with which the linear system can be completely described; i.e., the effect of a punctiform short-time stimulus $\delta(t)\delta_{i,\gamma,k}$ in a receptive field is to be measured in dependence upon k = 1, 2, ... , m at the i-th ganglionic cell, $\delta_{i,\gamma}$ is the Kronecker symbol. If one approximates the description of the system by the equations derived for the continuum and if the interconnection is described by Equations (19) and (19a) (to be extended to the two-dimensional case), then only four measurements are required. Two measurement values may be acquired from the limiting lines of the receptive outer field (H(r,s) = 0). A special difficulty of the measurement technique involved in determining the coupling function consists in the fact that frequently only dynamic measurements are possible; in this case Equations (27) and (28) can be used to determine the interconnection parameters.

2. According to Equations (26) and (27), an on-response arises whenever in a receptive field inhibition occurs with a time-delay as compared with excitation; in the converse case one gets an off-reaction (d). The dynamic reactions are thus network properties; the contribution of the receptors to the time-dependent responses of the system merely requires a quantitative correction which will be neglected in the following.

3. The time-delay of the excitation $T_1$ in the central region may be approximated by a low-pass filter of the first order; the value of $T_1$ may be derived in the case of stimulation with time-dependent jump functions, by multiple application of the equation

(46) $$y_a = \dot{y}\left(1 - e^{-\frac{t_a}{T_1}}\right)$$

while neglecting the background illumination, with the aid of the measured latency time $t_1$. The quantity $y_s$ denotes the threshold excitation at which the first pulse is triggered, $\hat{y}$ is the height of the jump function. Using the measured values from the cat we get

(47e) $$T_1 \approx 35 \text{ msec}.$$

The value is approximately the same if during excitation one assumes for the measured 15 Hz limiting frequency the limiting frequency of a simple low pass filter. If the time-delay for inhibition is likewise interpreted with the aid of a low pass filter then one gets, by determining the limiting frequency in the inhibitory outer field,

(48) $$n = \frac{T_1}{T_2} \approx 3.$$

The low pass filters at the input of the nerve cells determine very substantially the properties of the system. The time-dependent perturbation of the input signals may be very simply reduced to integration at the low pass filter [11, 12]; in addition the low pass filters, in the case of pulse shaped input signals, permit the construction of local filters with very much smaller numbers of synapses than would have been necessary if one had been dealing exclusively with the case of summation in the local region [11]. Besides, with the aid of low pass filters a simple form of motion detection is possible, as shown in Figure 8. The responses of the system to a jump stimulus $y(r,t) = \sigma(r)\,\sigma(t)$ may be described by Equations (26) and (27), where, in the measured receptive fields, one has the value $k = 1 - 3$ [sic]. In linearizable situations it is sufficient for the determination of the system parameters on the basis of Equations (26) and (27) to measure a jump response as a function of position at a specific point in time or as a function of time at a fixed position. The curves given in Figure 6 approximate the relationships in the cat-retina as functions of the coupling breadth $B_1$.

4. In the receptive field center inhibition and excitation have approximately the same response thresholds (m). For excitation at the same surface area there is a higher effective threshold in the boundary region than in the central region of a receptive field. This is explainable if one assumes that the coupling factors are smaller, in accordance with Figure 3, in the boundary region and that there the threshold s of the neuron in position (r,s) is first exceeded for higher values of excitation $y(r_0, s_0)$. At low intensities we can have, for stimulation in the boundary region,

(49) $$q = \frac{\int_{r_0-\Delta}^{r_0+\Delta}\int_{s_0-\Delta}^{s_0+\Delta} H(r-x, s-w)\, y(x,w)\, dx\, dw}{S} < 1$$

while in the center of the field at the same stimulus intensity we have q>1. From this it follows according to Figure 14 that the central region increases with the intensity and the extent of a small-surface stimulus. At higher ground-illumination the inhibiting effect of the outer field becomes effective since in the central region the effective threshold for inhibition is reduced in consequence of the outer field effect; the central region in consequence seems to be narrowed (f,g). At lower stimulus intensities the inhibition is practically eliminated and the retina is a low pass filter. The resolving power of the system is reduced (q). Besides the effect of the threshold, the low pass behavior of the system is further reinforced by the pulse structure of the signal, for at low stimulus intensities there is a reduction of the integrating effect of the synaptic time constants and the inhibitory effect becomes proportional to the probability that an inhibitory and an excitatory pulse simultaneously arrive at the membrane [11]. For the receptive field the characteristic of a ganglionic cell is obtained, in the case of surface illumination, in accordance with Figure 15, curve (a), by superposition of the threshold-dependent receptor characteristics. The differing thresholds for the effect of the receptors upon the ganglionic cell are caused by the distance-dependent drop in the coupling function which results in a higher effective threshold for distant receptors. The dynamic domain of the ganglionic cell is greater than that of <u>one</u> receptor. With increasing stimulus intensity, the then effective inhibition reduces the further rise in the characteristic of the ganglionic cell. By the combination of several ganglionic cells with differing thresholds the dynamic domain can be further enlarged (f, g).

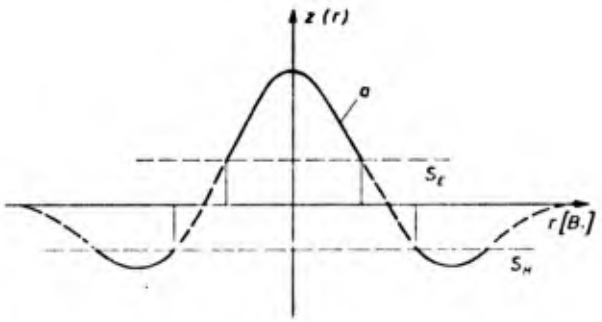



Figure 14. The effect of a small-surface stimulation of low intensity at the input of a neuron with radially symmetric coupling function. In the dashed region of the line (a) there occur, in consequence of the thresholds, no responses at the output of the cell.

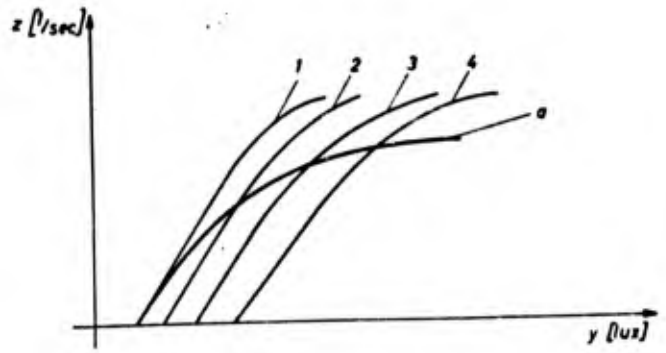
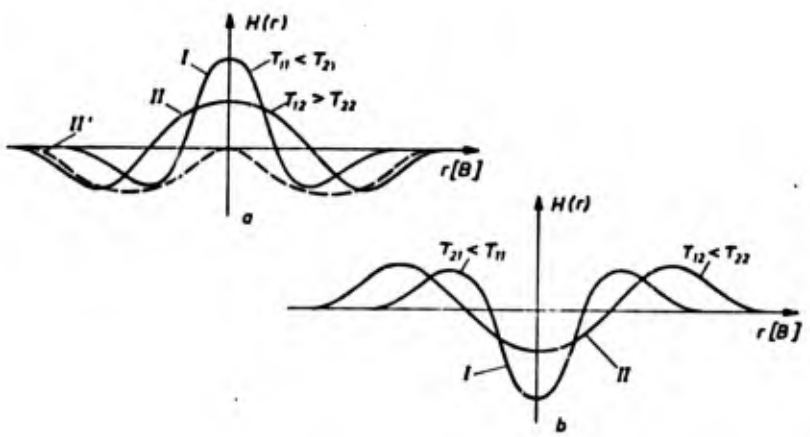



Figure 15. Characteristic of a ganglionic cell for surface stimulation (a); the curves 1-4 are characteristics of receptors at different positions in the receptive field.




Figures 16a and b. Coupling function of two ganglionic cells with positive (a) and negative (b) central region.

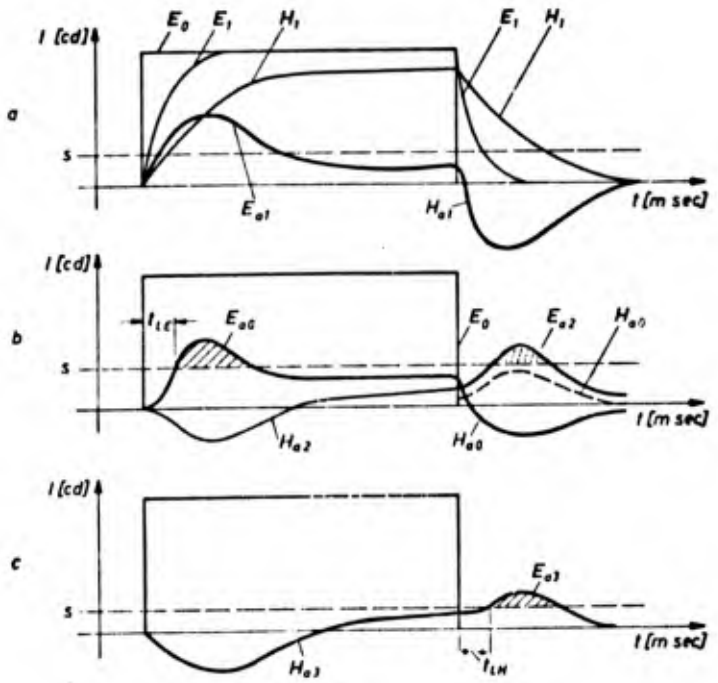



Figure 17. The production of time-dependent responses at the ganglionic cells as a result of the effect of excitatory (E) and inhibitory (H) input quantities. The shaded regions denote the intervals having measurable output quantities.

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5. In the cat's retina two inhibition-dispersion systems are superposed. The quantities $T_{11}$ and $T_{21}$ denote in system I the time constants of excitation and inhibition; in system II the equivalent quantities are $T_{12}$ and $T_{22}$. The system I, since $T_{11} < T_{21}$, causes the on-response in the center of the receptive fields. System II, owing to $T_{12} > T_{22}$, gives rise to the off-response in the boundary region (h). The times of latency of the responses of a cell to stimulation in the central region of the receptive field are independent of the sign of the effect, i.e., the off-reaction takes place in the field center with the same time of latency as does the on-response; the equivalent is true in each case for the contrary outer fields.

Figure 16 shows, for both cell types, the effective on and off systems which work together for a neuron with a positive central region in the following way:

For a short-time small-surface stimulus in the field center, according to Figure 17a, the responses $E_{a1}$ and $H_{a1}$ are formed by system I from the difference $E_1 - H_1$. In Figure 17b the corresponding curves $H_{a2}$ and $E_{a2}$ of the system II are plotted in accordance with Figure 16a; also plotted is the superposition of the responses of I and II to the total reaction $E_{a0}$ and $H_{a0}$, i.e., the real system generates an on-response since it is only capable of positive output values. In the boundary region of the receptive field, $H_{a2} > E_{a1}$ and $E_{a2} > H_{a1}$, so that an off-reaction $E_{a3}$ arises in Figure 17c. In the intermediate region of both parts of the field $E_{a1} > H_{a1}$ and $E_{a2} > H_{a1}$ so that both types of response occur (h). If one illuminates the entire central region then the off effect manifests itself more markedly and, on switching off, a response $H'_{a0}$ can occur. Reduction of background illumination reduces the effect of the outer field and in consequence the effective threshold S for the central region, so that $H'_{a0}$ can elicit an off-response although only the center is illuminated (i). An off-response in the central region can also be achieved at constant background illumination by increasing the stimulus intensity or the stimulus surface. The reason for this is the non-linearity of the characteristics according to Figure 15. In the given stimulus situation the system I operates further into the saturation region than does system II so that $E_{a2}$ increases more markedly with intensity than does $H_{a1}$ and an off-response takes place (i, j).

If simultaneously a stimulus is applied in the central region and also a stimulus is applied in the boundary region the quantities $E_{a0}$ and $H_{a3}$ as well as $E_{a3}$ and $H_{a0}$ interact upon one another. If the stimulus intensity in the center preponderates then we can have $Ha_0 > Ea_3$ and the off-response vanishes; if the boundary region is more strongly excited then the on-response vanishes since $H_{a3} > E_{a0}$; if both stimuli are equally strong then the on-responses and the off-responses must be reduced and the times of latency $t_{LE}$ and $t_{LH}$ must rise (k, l). The off-system could also have a coupling function in accordance with curve II' in Figure 16a. On the basis of observations made up to now it is impossible to distinguish between the two variants unambiguously. In addition to the dynamic responses, continuous discharges can also occur at higher ground illumination; this happens in particular whenever the difference between the excitation sum and the inhibitory sum in the steady state exceeds the threshold S (Figures 17b and c). The suppression of the response in the steady state is also interpretable if the systems designated "I" in Figures 16a and 16b operate together at the ganglionic cell; in this case the equivalent time constants of the two systems would have to be distinguishable. The quantitative description of the switch-on reactions presupposes the measurement of the coupling functions; the describing equations in linearizable cases are Equations (26) and (27) augmented by the equivalent expressions for system II. Figure 18 shows <u>one</u> possible interconnection schema of the retina which is based upon the histological researches of Poliak [16]. For neurons with positive field center the effect of the bipolars of the type $B_A$ preponderates in the central region; for cells with negative center, the bipolars of the type $B_B$ determine the responses of the central region.

6. The image on the retina is always in motion in consequence of the tremor motions (investigated mainly in man) and the saccades; in this way the mapping of the input pattern in the plane of the ganglionic cell layer is determined by the dynamic properties of the system. A qualitative assessment of the transformations may be secured with the aid of Equations (34) and (35). If for example an illuminated quadrilateral moves on the retina perpendicularly to an edge then in the system of the on-neurons according to Figure 8, curves b and c and Equation (34) the frequency of the ganglionic cells at an edge is increased and reduced at the opposite edge according to Figure 8, curve e and Equation (35) multiplied by (- 1). The cells having a negative central region produce the converse transformation (Figure 9b). As the motion-responses show, the maximum of the jump reaction becomes flatter with increasing velocity and is shifted away from the jump edge. Since the shifts for each field-type are in opposite senses, there exists the possibility of an elimination of this effect, as shown by Figure 10, curve b. The unsharpness which is bound up with the broader maxima must be eliminated in the system since the resolution attains -- at least at high contrasts -- the theoretical limit set by the distribution density.

The position-dependent responses plotted in Figures 8 and 9 correspond to the time-dependent reaction of a ganglionic cell in a particular location when the position coordinate is transformed into a time-dependent quantity. When irregular tremor motion and saccades occur it becomes possible, by using the field types which have been discussed, to heighten the contour lines of a pattern independently of the contrast direction. The ganglionic cells having positive and negative field-center thus make possible a common system for contrast amplification in which the local differentiation of the pattern is accomplished by means of a temporal differentiation, in part with the aid of motion. In Equations (34) and (35) $p \approx 0.2\text{-}2$ for the saccades. For the tremor motion there is approximately a range of $p = 0.05\text{-}0.3$. Both motions, according to Figure 11, lie in a region in which the ganglionic cells respond with an increase in frequency so that signals can be picked up in the geniculate body for the control of the saccade eye motions. Because of the complexity of the motions, an exact computational treatment of the problem in closed form is scarcely performable so that a treatment using model-nets is to be recommended (p, s). The numerical values employed have been measured in humans. A further treatment of the motion problem is carried out in Section 4.2.2.

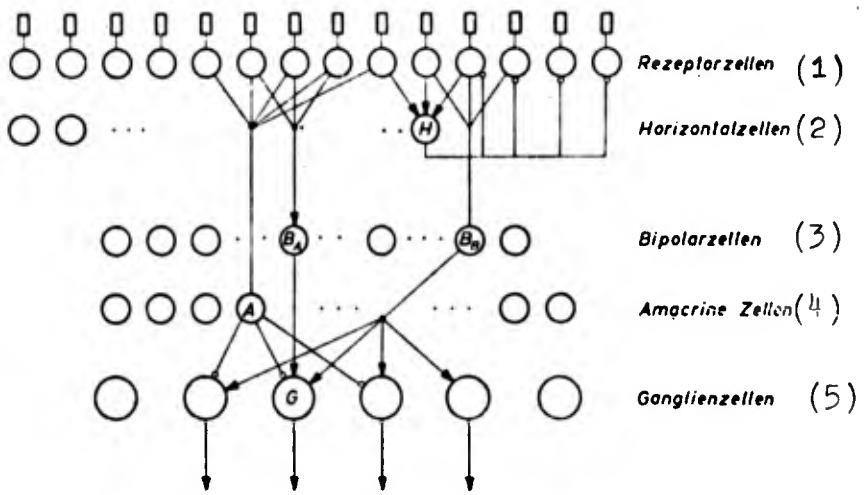


Figure 18. A possible interconnection schema, in the cat's retina, of neurons having positive center. In the central region fast bipolars ($B_a$) and slow amacrines operate together, in the boundary region slow bipolars ($B_B$) and fast horizontal cells determine the relationships of the situation.
Key:
1. Receptor cells.
2. Horizontal cells.
3. Bipolar cells.
4. Amacrine cells.
5. Ganglionic cells.

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7. In point 2-6 use is made of the frequency-dependence of the coupling factors in order to interpret the time-dependent responses of the retina. Since the ratio of the maximal fusion frequencies in flickering light for rods and cones corresponds, at a value of 1/3.5, approximately

to the ratio of the limiting frequencies of inhibition to [those of?] dispersion, the inhibition could be associated with the rods and the dispersion with the cones (n). In conflict with this view are histolc ical findings and the fact that in the electroretinogram the d-wave equivalent to the off-effect is, in cone-eyes, very much more pronounced than it is in rod-eyes (o). Hence it must be assumed that the receptors do indeed co-determine the dynamic responses of the system but that the time relationships are however determined essentially by the network of horizontal cells, bipolar cells, amacrine cells and ganglionic cells. The entire system displays pass-band behavior in the time domain as much as in the position domain, the mid-frequency lying at around 10 Hz (r). This pass-band characteristic of the system in the time-frequency domain is caused by the differing time constants of excitation and inhibition. The larger the difference $T_2 - T_1 = d$, the greater is the band width of the system; if the values of d are negative then there occurs ar inversion of the signal. Motion of the pattern has the effect of combining the frequency-response curves in the position-domain and time-domain with one another in the eye. Since the time-frequency-dependent filters are not constructable without a phase-frequency characteristic, motion of the pattern also gives rise to dispersion in the position domain. [Preceding sentence misprinted in original]. Equations (34) and (35) show -- taking as an example the transformation of a moving stimulus jump -- the effect of the combined position-time filtering. In Section 4.2.2 further properties of this system are investigated.

8. The contrasts measured in the case of moving lattice patterns and dependent upon the local frequency are in consequence of the motion of the stimulus (t) to be thought of only in a first approximation as local frequency-response characteristics in accordance with Equation (20); for the phase-frequency characteristic of the system is not taken into consideration. If one approximates the measured curves (t) with Equation (20) then coupling functions may be computed for inhibition and dispersion; these coupling functions are, like the local frequency-response characteristic, describable by the superposition of Bell curves. The ratio of the coupling breadths for inhibition and dispersion, k, turns out to be 3-4, the quantity $B_1$ lies in the range around 0.4°. The computed limiting frequencies amount to 1.2 oscillations per degree. The ratio of the maximal contrast sensitivity to the value at $\omega \to 0$ lies between 5 and 9. The remaining parameters of the coupling functions and of the frequency response characteristic are strongly dependent upon the particular structure of the experiment and are not suitable for further comparisons. The constant k can also be derived, using Equations (19), (19a) and (19b), from the size of the receptive partial fields associated with time-independent stimuli; one gets k = 1.0-3.0. The diverse values derived by the measurement methods show that further careful measurements are required.

The filter characteristic of the retina in the local region is exactly determinable only when a representative cross-section of coupling functions is derived. In humans, a rough approximation of the retinal local frequency-response characteristic is possible with the aid of psychophysical

measurements. For short presentation times (1.5 msec) of lattice grids, the local frequency-response characteristic of the entire visual system, measured with the aid of the subjective contrast threshold, corresponds approximately to that of the optical part of the eyes [9]. From this it follows that direct excitation reaches the cortex very fast in comparison with inhibition. If rectangular grids are presented for an interval of time which is of the order of magnitude of twice the retina time constants for inhibition (80 msec), then the local-frequency dependent contrast threshold must be essentially determined by the retina since the build-up time of the entire system in this experiment is about 1,000 msec [9]. The damping at low frequencies is a significant difference between the freqency-response characteristics for short presentation times and those for the steady state. The ratio of the contrast for a local frequency u = 1 line/mm at the retina to the maximal value for u = 20 lines/mm amounts to 0.40 in the steady state and 0.65 for a presentation time of 80 msec. For the cat the ratio in the steady state is of the order of magnitude of 0.2 [19]; hence there must be a more marked contrast-magnification even at the ganglionic cell level than there is in the case of man. The observations under discussion do no admit of any exact quantitative comparison.

9. In the vertebrate eye the environment is mapped on the receptor grid of the retina. The distribution density in the area centralis corresponds in man to the limiting value given by the wave-optical mapping. By means of a neural network the input pattern is transformed into a local distribution of time-dependent pulse frequencies in the plane of the ganglionic cells. The layer [level?] of the ganglionic cells represents the superposition of two systems which are characterized by receptive fields having a positive (or negative) central region and an outer field operating in each of these two cases with the opposite sign. The entire system, when the active motions of the eye are included, possesses pass-band character for local frequencies and time-frequencies. From this it follows that both locally dependent and time-dependent changes in the input brightness distribution are detected especially well. In the local region this property results in an emphasis of the pattern contours in the plane of the ganglionic cell layer. The determination of the basic brightness probably is carried out by a special low pass system of neurons whose receptive fields are particularly large. From findings made hitherto it is impossible to infer how well the linear formulations describe the system regionally and what information is eliminated, because of the presence of non-linearities, even at the ganglionic cell level. From the fact that at low stimulus intensities the pass-band system becomes a low pass system it may be inferred that the linearizable region of the system is markedly restricted at these intensities; for the low pass behavior of the eye, which arises because of the absence of inhibition, is to be attributed to the thresholds of the neurons and the pulse structure of the signal [11], which is especially effective at low intensities.

## 4.2 The Geniculate Body.

After the retina, the geniculate body is the second switching position in the visual system. In this part of the brain information from the contralateral half of the one eye and the ipsilateral half of the other eye is brought together (Figure 1). The geniculate body is connected with the area striata and the regions of the brain which play an essential role for the motoricity of the eyes.

### 4.2.1. Experimental Results.

a) The geniculate body consists in primates of six, in the cat of three levels (Figure 1). In the latter animal the upper and the lower levels of the outer half of the eye are associated with half of the geniculate body on the same side, the middle level is in each case connected to the nasal half of the other eye [20, 16].

b) In the geniculate body the input brightness distribution is mapped in the form of a position-dependent spike distribution. The cells of the geniculate body have receptive fields structured similarly to those of the ganglionic cells; fields with positive central region and negative central region occur with the same frequency and are markedly overlapped [16, 20].

c) Leads from cells which lie below one another perpendicularly to the surface associate the receptive fields in all layers to the same positions of the one eye or to the equivalent locations in the other eye [20].

d) The geniculate cells react more weakly to diffuse illumination than do ganglionic cells [20].

e) The inhibitory effect of receptive outer fields is more pronounced in the geniculate body than in ganglionic cells; the drop-off of the coupling functions is frequently steeper and the central region smaller [20].

f) On the average around 10 ganglionic cells in the region of the area centralis are connected with one neuron of the geniculate body [16].

g) In the geniculate body no cells have been found which are unquestionably capable of being influenced by both eyes [20].

h) The reactions of the geniculate cells exhibit pronounced group formations of nerve impulse sequences [20].

i) If the retina is stimulated by light flashes of 25 msec duration in such a way that the stimulus lies just above the threshold of the geniculate neuron then the geniculate cells may be divided into three classes relative to their times of latency. The following times were measured with the frequencies shown: 1.90 msec (60%), 2.17 msec (24%), 3.27 msec (16%) [21].

j) Upon stimulation of the retina with moving strip patterns for which position-dependent sinusoidal brightness distributions exist in the direction of motion, the responses of geniculate cells are dependent upon the local frequency of the input pattern. The curve profile measured in this way displays, for the neurons investigated, a pass band character with a drop-off at high frequencies which is approximable by a bell curve. The motion of the stimulating pattern was so selected that the number of maxima in the time unit at one point of a receptive field was independent of the local frequency of the stimulus. The size of the velocity selected permitted an acoustic perception of the impulse frequency of the neurons modulated by the input stimulus. The thus measured limiting frequency of the geniculate neurons lies, at 0.9 oscillations per degree, below the limiting frequency of the ganglionic cells [22].

4.2.2. Discussion of the Results.

1. The geometric arrangement of the layers can be a prerequisite for binocular vision; however the information processing required for this purpose does not take place in the geniculate body (a, g). Since equivalent points of both eyes lie in consequence of the mapping, above one another in the geniculate body the stimuli can be combined with one another (see Section 4.3.2) by simple position-dependent summation in the vertical direction in the following processing stage.

2. By simple dispersion in a second neuron plane, the receptive fields of the cells are magnified in comparison with the input plane. However, despite the presence of dispersion (f), the central regions of the receptive fields in the geniculate body are smaller rather than larger (e) and the total system is insensitive with regard to diffuse illumination. From this it follows that in the geniculate body a further inhibition connection occurs.

3. In consequence of this additional inhibition and of the steeper drop-off of the coupling functions with a smaller central region the total system acquires, in accordance with Equation (20), a more strongly pronounced band-pass character with increased damping in the region of lower local frequencies. The receptive fields with positive and negative central region probably function together, as in the retina, as a filtering system (b, d, e, f).

4. In the event that the nerve pulse group-formation occurring in the geniculate body has not been produced by anesthetics but is signal-dependent, such group-formation can be interpreted in two ways. On the one hand it is possible for the coupling factors $b_{ij}$ to be greater than 1, on the other hand a system involving pulse-frequency modulated signals tends toward time-dependent oscillations which manifest themselves in variable instantaneous frequency if the neurons of the system are interconnected according to the principle of backwards inhibition [11].

5. The times of latency of most geniculate neurons lie in the range of times which have also been observed for the retina (see Section 4.1.1e); from this it follows that in the geniculate body integration in the time domain is only slightly present. The relatively few dispersion interconnections (f) and the occurrence of spike groups, taken together with the shortness of the latency time, suggest the conclusion that no backwards inhibition is present but that the coupling factors are greater than 1. Results up to now have shown that the geniculate body plays no essential role in the information processing of form vision. The input brightness distribution is band-pass filtered by the retina and the geniculate body in the local domain and conducted to the visual cortex for the actual form analysis.

6. If one neglects the phase-frequency characteristic of the retina-geniculate system during stimulation with moving strip patterns, then the measurements described in (j) should be interpreted in a first approximation as local frequency-response characteristics. The measurement curves can be well approximated according to Equation (20) as the difference between two Gaussian curves. The limiting frequency amounts in the mean to 0.9 oscillations per degree. The reduced limiting frequency relative to the retina is caused by dispersion in the geniculate body. If one determines the associated coupling functions from the frequency-response curves then one gets 3 - 4 for k and $m_1/m_2 = 4$. Since the authors [22] give no exact data regarding the drift velocity of their patterns it is not possible to make a precise comparison with the measurements described in Section 4.1.1 (t). The damping of low local frequencies appears to be more pronounced for geniculate neurons than for ganglionic cells (d, j). In addition to the neurons having band-pass characteristics in the local region, cells having a pronounced low pass behavior also occur there. An association of the times of latency (i) and the local frequency-response characteristics at a neuron has thus far not been successfully accomplished experimentally. From the situation discussed in Section 4.1.2, point 9 it may be inferred that the position-dependent low pass filters build up to steady state more rapidly in the time domain than do the band-pass filters.

In very many cases one gets exclusively dynamic responses at the cells so that the system-describing Equation (20) is replaced by Equation (30). If it is possible to measure the local frequency-response characteristic with moving grid patterns in a manner corresponding to (j), then all interconnection parameters can be derived with the aid of Equation (30).

Part 2 of this paper appears in Vol. 7, No. 3.